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XIX.—*On the Adaptation of Mammals to Aquatic Life.* By Dr. Willy Kükenthal, Ritter-Professor of Phylogeny in the University of Jena *.

The organization of the mammal is fitted for the life on dry land, just as that of the fish and the bird is adapted to an existence, in the one case in the water, in the other in the air; and we can form a good idea of the intensity of the struggle for existence when we observe how large a number of mammals has been driven from the surface of the land. The majority of the orders belonging to this class contain representatives which have adopted either a burrowing subterranean, an aerial, or an aquatic mode of life. The latter especially is of frequent occurrence, and we see how entire orders of mammals, such as the Whales, the Sirenians, and the Seals, have been driven into the water. Orders too, otherwise terrestrial, contain solitary representatives which have abandoned the terrestrial life, such as *Platypus* among the Monotremata and *Chironectes variegatus* among the Marsupialia, while among the Rodents we have a larger number:—

* Translated from the 'Zoologische Jahrbücher,' Abtheilung für Systematik, Geographie, und Biologie der Thiere, Bd. v. Heft 3, Jena, October 1890, pp. 373-379.

the Yellow-bellied Water-Mouse (*Hydromys chrysogaster*);
Holochilus;
the Water-Vole (*Arvicola amphibius*);
the Musk-Rat (*Fiber zibethicus*);
the Beaver (*Castor fiber*); and
the Capybara (*Hydrochœrus capybara*).

Among the Insectivora:

the Water-Shrew (*Sorex fodiens*) and
the Desman (*Myogale*).

Among the Ungulata (Artiodactyla):

the Hippopotamus (*Hippopotamus amphibius*).

Among the Carnivora:

the Otter (*Lutra*) and
the Sea-Otter (*Enhydris*).

On a closer examination of these more or less exclusively aquatic creatures we find that, notwithstanding the variety of orders to which they belong, they nevertheless possess many common structural features, and we shall be perfectly safe in ascribing these points of agreement to the influence of the aquatic life.

Owing to adaptation to the life in water, therefore, changes have taken place in the organization of these animals. The extent of these changes will vary in direct ratio with the time during which the influence of the water has been operating; or, in other words, the changes will be greater or less according as a longer or shorter time has clapsed since the animals in question exchanged the terrestrial for the aquatic life. We have further to consider that many of the aquatic mammals which we have enumerated live by no means entirely in the water, but are at times land-dwellers as well. The next point to be ascertained is whether these changes are always manifested in the same direction.

In the case of a large number of forms, in order to become acquainted with the changes which have taken place, it is sufficient to compare the animals with their nearest relations on land. But, as a matter of course, closely allied terrestrial forms are to be found in the case of those mammals alone which have only recently adopted the water as their element; those which have been aquatic for a long time will be able to show no relations on land, since both the water as well as the land branch have struck off from one another in diverging directions. Thus we are at once able to assign the water-rat to the voles (Arvicolidæ), the otter to the martens; but of the seals we are only able to say in a general way that they are allied to the Carnivores, as the Sirenians are to the Ungulates; while of the relationships of the typical aquatic mammals, the whales, we at present know nothing. Not that no hypotheses have been set up to explain the origin of the whales! The question of their descent has been largely ventilated, and the majority of the zoologists who have attacked the problem have not been behindhand with their answer. Let us pass over for the nonce the views of the older authors, and devote ourselves to the most modern theories of the phylogeny of the Cetacea!

Some naturalists consider the whales to have sprung directly from the hypothetical Pro-Mammalia, and to be therefore closely allied to the Reptiles, basing their hypothesis on similarities in structure, particularly with certain extinct reptiles, the Ichthyosauri; others place them near the Ungulates, with which they are supposed to be connected through the Sirenians. By other authors, again, the whales are held to be allied to the seals or to the Carnivora in general; nay, they are even said to lead to the seals through the Sirenians; and of the most recent workers at the group, one (Weber) comes to the conclusion that the whales possess certain characters pointing to affinities with the Carnivora, particularly with the seals, and others which suggest a relationship to the Ungulates; while the other investigator (Leboucq) is convinced, from the results of his work on the flipper, that in the whales we have extremely ancient mammals, whose ancestors never lived on land, but were only swamp-dwellers.

This is briefly what the most modern theories of the phylogeny of the whales amount to, and the views expressed are so divergent as not to convey an exalted idea of the present position of phylogenetic science. The thought involuntarily strikes us whether the method of phylogenetic inquiry may not in this case be somewhat inefficient. If we follow in detail the path which the various investigators, among them the foremost zoologists of the age, have each one pursued, we find that, of the various methods of obtaining phylogenetic knowledge, it has always been that of comparative anatomy which they have adopted, and that it has ever been similarities in structure with another group of animals which have persuaded them, according as they attached greater or less importance thereto, to connect the whales with the Ichthyosaurs, the Seals, or the Carnivores, with the Sirenians or the Ungulates.

Here lies, in my opinion, the chief weakness, from which all these hypotheses suffer; for we can quite easily conceive that two animals which exhibit many points of structural agreement may nevertheless not be allied to one another, but, as branches of two perfectly distinct orders, have gradually acquired similar characteristics through similar adaptation. It shall be my task to prove this with special reference to the hand of the aquatic Mammalia.

It must be laid down from the outset as a fundamental principle that all mammals living in water have sprung from terrestrial forms. It is not merely considerations of a general nature which lead to the advancement of this proposition; the proof has also been furnished in detail with the greatest certainty, and there is scarcely anything new to add to it *.

We will now, omitting a detailed account of the resemblances which have resulted from the adaptation to an aquatic existence, devote our attention in the first place to a brief general consideration of the external bodily form. It is doubtless hardly necessary to draw especial attention to the purely hypothetical nature of this method of examination.

All water-mammals have acquired a more fish-like form the longer and the more exclusively they have adapted themselves to the aquatic mode of life. There is no question thereby of any retrogression; the elongated, gradually diminishing form of body is the most practical for all vertebrates which move by swimming.

One section of the aquatic Mammalia is permanently confined to the water; another periodically spends a longer or shorter portion of its life on land, and from this there arises a highly important difference. In the case of those animals which dwell for a time upon dry ground we shall find that the extremities have not become so entirely adapted to the functions of swimming as in the case of the others. Anterior as well as posterior extremities are used upon the land as legs and in the water as paddles, and the principal alteration which we notice in animals of this class consists in an increase in the size of the hind limb, which, for mechanical reasons, is more utilized in swimming than the anterior extremity. This difference in size may be often noticed in very pregnant fashion in the case of the aquatic Mammals to which we have alluded.

In the case of those animals which remain permanently in the water the function of the extremities as ambulatory organs entirely disappears, and we are confronted with a modification which is of great importance for locomotion in water, in that

* For the Cetaceans see, for instance, Weber, "Ueber die cetoide Natur der Promammalia," Anatomischer Anzeiger, 1887, p. 42.

the tail supersedes the posterior extremities as a motive organ. This new method of locomotion, which possesses as great an advantage over the movement by means of the extremities as does the screw-steamer over the row-boat, brought into existence two very noticeable changes in the form of the body —in the first place the loss of the hind limbs, and then the transformation of the tail by expansion into a caudal fin.

In the case also of many temporarily aquatic animals the tail has already begun to take part in the function of swimming, and in consequence thereof has undergone an expansion, which is in most cases horizontal, as in the platypus or the beaver, the musk-rat and the desman alone possessing a laterally compressed tail. Nevertheless the functional importance of the caudal extremity cannot outweigh that of the hind limbs, since the latter are essential to the power of locomotion upon dry land which these animals possess.

The transition from the one principle to the other can be beautifully traced in the case of the seals; for the eared seals pass a relatively large proportion of their time on land, and consequently their hinder extremities still possess the power of locomotion, their position with relation to the body is similar to what obtains in the case of other land-animals, and in the water fore and hind limbs are equally utilized in the action of swimming. The true seals, on the other hand, live much more exclusively in the water, and therefore the function of swimming predominates and is transferred to the hind limbs, which, projecting from the body posteriorly, have assumed a tail-like shape and perform similar movements to those of, let us say, the tail of the whale, while the fore limbs relinquish the functions of mere oars, and are employed more for the purposes of balancing and turning.

The new method of motion attains its highest development in the Sirenians and the whales; the powerfully expanded caudal fin has become the sole motile organ, the anterior extremities functioning henceforth as rudders. We therefore see that in the practice of swimming by the series of aquatic mammals a new principle is gradually evolved, in that the motive power is transferred to the hinder end of the body, the consequence of which is the assumption of a more and more fish-like form.

The lines which we must consider the phylogenetic development of these processes to have followed have already been traced in a masterly manner by Roux *. According to this

* W. Roux, "Beiträge zur Morphologie der functionellen Anpassung. —I. Structur eines hoch differenzirten bindegewebigen Organes (der Schwanzflosse des Delphin)," Archiv f. Anat. u. Physiol. 1883, p. 76.

author the only new element necessary for the earliest origin of the dolphin's caudal fin, as well as the attainment of its highest perfection, consisted in rough embryonic variations, which presented something approaching the form of a fin-like appendage, so that therefore this new formation is to be regarded as the product of individual selection in the Darwinian sense. The internal structure of the caudal fin of connective tissue, which is so extraordinarily practical and constructed according to mechanical laws, cannot, on the other hand, be explained by means of selection alone; it is a functional adaptation, a specialization of the qualities of the tissues.

What we have thus far established is this: in consequence of adaptation to the aquatic life the external form of the mammals concerned assumes a special fish-like shape; this transformation is intensified in the case of those mammals which remain permanently in the water, for in them a quicker and more agile motion is obtained by the substitution of the complicated lashing action of the tail for the oar-like action of the extremities. Every function of the hind limbs is suspended, and they therefore disappear, while the tail undergoes that expansion by which its utility is increased, and so becomes the caudal fin. In the case of the seals a transition is observable, in so far as one division, the true seals, use the posterior limbs in swimming in a similar manner to that in which the whales use their tail. It may here suffice to state that, from the standpoint of comparative anatomy, the attempt has been made (Ryder)* to explain the caudal fin of the whale and the hind feet of the seal as homologous structures.

Thus we see how similarity of outward form results from similar adaptation, in the present instance to life in water; and in the various aquatic mammals, to which we have alluded, we can trace this in all its varying stages.

These phenomena appear more distinct and applicable as direct proofs when we select separate systems of organs for the purpose of examination. It seems simplest to select the external body-covering of the aquatic mammals for the purpose of examination. We may state forthwith that great differences will be found between temporarily and permanently aquatic mammals as regards the partial transformation of the integument. Temporarily aquatic mammals, for instance, cannot do without a covering of hair, which to the others becomes a useless encumbrance. The changes which we

* John Ryder, "On the Development of the Cetacea, together with a Consideration of the probable Homologies of the Flukes of Cetaceans and Sirenians," United States Comm. of Fish and Fisheries, 1885, p. 427.

observe in the integument of the former are therefore comparatively small. They retain a thick fur of short close-lying hair, which, being well impregnated with grease, preserves the skin from saturation and also from loss of moisture when the animal leaves the water. In consequence of the more equable temperature of the water the shedding of the coat does not proceed so vigorously as in those of the nearest allies of these creatures on land.

Now while in the case of those animals which only seek the water for short periods the hair is quite efficient for the purpose of regulating the radiation of heat from the body, it is not so in the case of those which remain in the water for a longer time. Water is a better conductor of heat than air, and we therefore see how animals, especially where the temperature of the water is low, as in the polar regions, are clothed with a layer of fat lying beneath the cutis, which checks the radiation of heat better than could a coat of hair. The more absolutely the animal adapts itself to the life in water the less will be the use of the hairy covering, owing to the shortness of the stay on land; and, as a matter of fact, in the order of seals, hand in hand with the biological observations of the longer or shorter time spent on land by the various species, we can determine the presence of a denser covering of hair or detect a thinning of the coat, corresponding with the gradual increase of the layer of blubber.

In those mammals which live entirely in the water the coat of hair disappears. Thus adult Sirenians exhibit only scanty vestiges of such a covering, while their embryos still exhibit traces of a thick coat of hair extending over the whole body, including the limbs and tail.

In two embryos of *Manatus*, respectively 11 and 26 centim. long, I find the following appearance:—The integument of the smaller of the two is still smooth, with the exception of a number of regularly arranged small brown papillæ, which are gathered together on both sides of the upper lip; in the larger specimen fine stiff hairs project from the papillæ, which are disposed in longitudinal rows, and the external coat now acquires a resemblance to that of the Indian elephant, in which likewise stiff hairs about 1 centim. in length are arranged at certain intervals from one another in longitudinal rows; but besides this, the skin of the embryo of *Manatus* exhibits a vast number of very fine openings between the papillæ, which must be regarded as the mouths of follicles belonging to finer hairs. The anterior extremities and the tail also exhibit this hairy covering. On both sides of the upper lip the vibrissæ, which persist in the adult, have grown stronger. Precisely similar relations are found in *Halicore dugong*. A large embryo, 5 feet 4 inches long, described by Turner *, shows, besides isolated silky hairs arranged in rows and more numerous on the head and trunk than on the limbs, follicle-mouths closely packed between these, belonging to very fine hairs which have not appeared.

It follows that there can be no doubt that the Sirenians have sprung from animals with a thick covering of hair.

A precisely similar hairy covering is also found in the hippopotamus †. While old specimens possess thick bristles upon the upper and under lip, which become sparser on the dorsal surface of the head and trunk, the skin of the head and neck of a new-born animal exhibits a tolerably thick coat of lanugo-like hairs, which therefore subsequently disappear. But the whales also show vestiges of a former hairy coat, and in this respect the Balænoidea are most noticeable; even in adult animals solitary stiff bristles are still to be found in the cephalic region.

In a rorqual (*Balænoptera musculus*) 62 feet long I found at the tip of the lower jaw a triangular patch, 15 by 6·5 centim., of regularly arranged pits, which are to be regarded as the remains of hair-follicles. These pits, which were about 2 millim. broad and 1 millim. deep, were disposed in about a dozen rows, the longest of which contained twenty-six pits. The terrestrial ancestors of the whalebone whales therefore, besides having a coat of hair over the whole body, also possessed a thick tuft of vibrissæ upon the chin, much in the same way as the walrus or the bearded seal bear them on both sides of the upper lip in front. Embryos of the latter animals exhibit areas of pits in this region, just as regularly arranged as in the adult rorqual.

On the body of the same rorqual I found scattered hairs arranged as follows:—On the upper jaw they stood in rows close to the mouth; nearer the dorsal region they got more irregular, and disappeared behind the blow-hole. The lower jaw likewise possessed hairs arranged in three rows lying one above the other on each side; those of the lowest row in particular were surrounded by rings of pigment about the size of a cherry. The distance between each hair was about 1 foot.

Nearly all these brittle hairs, which were about one inch in

* Turner, "On the Placentation of *Halicore dugong*," Trans. Roy. Soc. Edinb. vol. xxxv. part 2 (1889).

† *Vide* Weber, "Ueber die Haut von *Hippopotamus amphibius*," Studien über Säugethiere, Jena, 1886, p. 3.

length and darkly pigmented on the upper jaw, but pale on the lower, sprang not directly from the surface of the skin, but were sunk in deeply pigmented pits. Such pits were moreover to be found spread over the body as far as the middle and especially numerous on the back, yet without any hairs springing from them. Some were deeper, some shallower, some merely indicated by a spot of pigment. We are therefore entitled to say that the last vestiges of a hairy coat are found on the entire anterior half of the body in the adult rorqual.

In the whalebone whales the remains of a former covering of hair are still quite distinct; in this respect a sharp contrast is afforded by the toothed whales, which (with the exception of *Inia*) possess no hairs in the adult state, and in embryonic life only a few tactile hairs on both sides of the upper lip. That even these may be absent is proved by the white whale and the narwhal, in which not even traces of hairs are found at any period of their development.

Throughout the series of aquatic mammals we have learnt to recognize the reduction of the hairy coat as a striking phenomenon of adaptation, and have been able to follow its disappearance step by step both with the aid of comparative anatomy and also developmentally. The more the animals develop from temporary into permanent inhabitants of the water, of less use does the coat of hair become; owing to the change of medium and consequent better conduction of heat, it is no longer sufficient to protect the body from loss of warmth, and it is superseded by the layer of blubber beneath the skin.

The further phenomena of adaptation as seen in the skin are of a more secondary nature; integumentary glands, smooth musculature, and integumentary nerves undergo gradual reduction, ending in complete disappearance.

Now in wishing to institute investigations into the relationships of these animals we must not adduce the similarities to be found in the structure of the integument as proofs of their affinity; for these converging resemblances have arisen independently of one another. The influence of the aquatic life on the integument manifests itself in the same direction. Only those features can be used as phylogenetic connecting-links which have persisted independently of these influences.

Still confining our attention to the whales, we at once find a marked difference within the order, in that the bearded whales throughout exhibit a relatively much richer covering of hair than the toothed whales. The mode of life of both is precisely similar, and we must therefore conclude that the bearded whales have not been exposed to the influence of aquatic life so long as the others.

A second and quite fundamental difference between the integument of the two groups lies in the appearance in the toothed whales of remains of a dermal armature *.

A whale which inhabits Indian rivers, *Neomeris phocænoides*, exhibits on the dorsal surface a large number of plates, regularly fitted to one another and each bearing a tubercle. These closely adjoining plates form a long narrow area, besides which plates still exist on the anterior margin of the flippers and round the blow-hole. That we are here not dealing with a casual malformation is shown by the embryology of the animal; for in an embryo of this rare whale we find in place of the dermal scutes, in precisely the same position, tubercles which cover the body to the number of many hundreds, and on its anterior portion are arranged in rows.

It might here be asked, "Is this appearance ancestral or something newly acquired?" Reasoning by analogy we must decide in favour of the former. In the first place there are a number of reptiles which are undergoing the loss of their dermal armature in precisely the same way, e. g. *Heloderma* or *Dermochelys*, the rudiments of whose dorsal coat of mail are found in the embryo as a number of longitudinally disposed rows of tubercles; secondly, palæontology affords us direct proof that the dermal armature of terrestrial ancestors disappears through adaptation to a pelagic mode of life. We must therefore regard the appearance described in *Neomeris* as a dermal armature in process of degeneration.

This conclusion coincides with the view that the group of whales originated in fresh water. *Platanista* and *Inia* also have preserved certain tolerably general mammalian characteristics †.

In this way, too, certain recent statements are rendered intelligible, according to which tubercles occur on the back, in point of fact on the anterior edge of the dorsal fin, in porpoises, the near allies of *Neomeris*. While the common porpoise (*Phocæna communis*) possesses only a single row of such tubercles, they run in three rows along the dorsal fin of another species (*Phocæna spinipinnis*). In the porpoises therefore we find the last vestige of that dermal armature which is still so distinctly developed in *Neomeris*.

One conclusion only is possible from what has been stated,

* Kükenthal, "Ueber Reste eines Hautpanzers bei Zahnwalen," Anat. Anzeiger, 1890, no. 8, p. 237.

† *Cf.* W. H. Flower, "Die Wale in Vergangenheit und Gegenwart und ihr wahrscheinlicher Ursprung," Kosmos, Bd. xiii. 1883, p. 531.

namely that the ancestors of the toothed whales were terrestrial animals with a dermal armature. It follows from this that on the one hand a great gulf is fixed between the whalebone and the toothed whales, and that on the other we must relinquish all attempts at bringing the toothed whales into any close relation whatsoever with the Ungulates or the Carnivores. The toothed whales branched off from terrestrial ancestors at a time when the latter still possessed an exoskeleton of epidermic scales, such as, for instance, a division of the Edentata still bears as, perhaps, an ancient heirloom. I would here like to quote a statement made by Baume when discussing the question whether the carapace of the armadillo is or is not acquired:—"There is nothing to prevent us from deriving the Mammalia, including even the Placentalia, from armour-bearing ancestors" *.

As a new instance of adaptation to the aquatic life we have now learnt to recognize the gradual disappearance of the dermal armature of terrestrial ancestors. It is not only in the group of toothed whales that this is seen; we already find the same phenomenon at an earlier period of the earth's history. It is assumed by recent investigators that the Ichthyosauri, which were pelagic animals, sprang from land-inhabiting reptiles. According to Fraas † the epidermic exoskeleton has disappeared in these creatures, with the exception of remains of horny scales, which are to be found on the anterior margin of the paddles (as in *Neomeris*). "The integument of the *Ichthyosaurus*, as has been clearly proved by our discoveries, was a completely naked and deeply pigmented skin, for the most part entirely without an armature of scales, whether horny or bony plates, with the exception of a region on the front margin of the paddle, which was protected by a longitudinal row of horny scales."

A more perfect analogy could hardly be found. On the one hand in the reptiles, on the other in the mammals, the dermal armature has been lost owing to adaptation to the aquatic life; in both cases it persists in a vestigial condition on the anterior margin of the flippers. The reason why the remains of the armature should have persisted so long at precisely this point is readily understood when we reflect on the speed with which these animals cleave the water and the necessity for keeping these parts of the body rigid.

The comparative examination of the integument of the aquatic mammals proved to us how it was possible for resem-

* Baume, 'Odontologische Forschungen,' Leipzig, 1882, p. 197.

† E. Fraas, "Ueber die Finne von *Ichthyosaurus*," Jahreshefte Ver. für Vaterl. Naturkunde in Württemberg, 1888.

blances to arise owing to convergence, and to be therefore of no value in tracing phylogenetic affinities. Moreover the differences in the structure of the skin in the case of the whalebone and toothed whales came into much greater prominence after the results of convergence had been eliminated. On the ground of these differences alone we are justified in maintaining that the toothed whales are of much earlier origin than the whalebone whales, and that the terrestrial ancestors of the two divisions were not identical; and with this we arrive at the first justification for the assertion that *the whales are of diphyletic origin.*

This assertion admits of being proved equally well with the help of other systems of organs. The fore limb appears to be particularly well adapted for this purpose.

The great difference which we noticed even in the skin of aquatic mammals, according as the particular animals were exclusively water-dwellers or merely amphibious, is intensified in the case of the fore limb. It is not until we reach the animals which pass the whole of their time in water that we find the fore limb developing into a fin. The tendency towards the formation of swimming-membranes between the digits is common to all the water-mammals. In exact ratio to the degree of general adaptation to aquatic life do we find this membrane either just indicated, or uniting the digits, or finally enveloping them so that they are no longer visible from the exterior. The comparative anatomy of the creatures which we shall now proceed to indicate exhibits the progressive development of the swimming-membranes. In a certain number of aquatic mammals, such as *Arvicola amphibius*, *Hydromys chrysogaster*, *Fiber zibethicus*, and others, no swimming-membranes whatever are to be found; others, as *Hydrochœrus*, possess rudiments; others, such as the beaver, have webs on the hind feet only, which then have to perform the bulk of the work in swimming; others again, as *Ornithorhynchus*, *Lutra*, and *Enhydris*, have webs reaching to the claws on the fore as well as on the hind feet; while in the case of others the swimming-membranes are expanded by means of strands of connective tissue which project beneath the terminal phalanges, as in the Pinnipedia, until finally the whole fore limb is enveloped in the swimming-membrane, as in the Sirenians, which still show traces of nails, and in the whalebone and toothed whales, which have lost even these. Leboucq's * statements about rudiments of nails having been

* Fl. Leboucq, "Recherches sur la morphologie de la main chez les mammifères marins," Archives de Biologie, tom. ix., 1889.

found in embryos of the latter seem to me not wholly free from doubt.

In the land-mammals the various divisions of the fore limb have different functions, to which they are adapted; the structure of these divisions is consequently not the same, but rather each is adapted to its own particular function. Now as the fore limb comes to be used more and more as a fin the degree of differentiation of the various parts diminishes, their functions are more nearly the same, and the consequence of this will be that skeleton and musculature will both be influenced thereby. As a matter of fact we can trace the loss of differentiation between the various skeletal parts of the hand in the series of aquatic mammals, while at the same time there sets in a gradual reduction of the joints which bind these parts together. The changes therefore which the anterior extremity has to undergo in the process of being transformed into a flipper rest on purely mechanical grounds. On similar grounds it appears more advantageous for the long phalanges to become somewhat more flexible. Now how is this brought about?

We all know that the ossification of the finger-joints takes place in such a way that each skeletal element is preformed in cartilage, in the middle of which there subsequently appears a bony centre, the diaphysis. The ossification of one of the cartilaginous ends now proceeds from this diaphysis, while the other, the epiphysis, receives a separate osseous germ of its own, which does not unite with the diaphysis until later. *Now in order to produce more flexible elements an incomplete ossification takes place in the aquatic mammals; a retardation of the process sets in.* This retarded ossification shows itself primarily in the diminished size of the diaphysis and the increased size of the epiphysis, while the latter unites with the former either only incompletely or else not at all. Of this we have a whole series of instances among the aquatic mammals. At the same time, however, a retardation also sets in in the ossification of the other end of the joint; the formation of the diaphysis is already to a certain degree completed, while this end still remains cartilaginous; finally a separate osseous germ will appear in it, and so we have the formation of double epiphyses. We find indications of these double epiphyses in the metacarpals of *Platypus*; we find them further advanced in the hands of seals and Sirenians, and fully developed in the whalebone and toothed whales.

That it actually is an instance of adaptation to the aquatic life with which we are dealing, is proved by the fact that it is only in aquatic mammals that double epiphyses are found.

If we examine the extent to which this phenomenon occurs in the fore limbs of each of the aquatic mammals which I have enumerated, we shall find that the skeleton of the manus has undergone least modification in those animals which exhibit least material modifications in other respects also, the only noticeable change being that the epiphyses become larger and more distinct.

In *Hydromys chrysogaster* and *Hydrochœrus capybara* the ossification is slightly more tardy, and we already perceive indications of double epiphyses, just as in the metacarpals of *Ornithorhynchus*; in the case of the otter it has already been remarked by Allen Thomson * that "the ossific union of the epiphyses in these animals seems to be comparatively tardy." In the case of the beaver this is equally true. We have therefore a whole series of transitions between hands with one epiphysis and those with two epiphyses on each finger-joint. As for the seals, it has been stated by Weber †:—"In the Pinnipedia the ossification of the hand takes place on the usual plan, in that proximal epiphyses only are developed; in the foot, however, all the phalanges, with the exception of the last, have a distal epiphysis in addition to the usual proximal one." This assertion is not strictly accurate; it has already been stated by Flower, in his 'Osteology of the Mammalia,' ‡ that *Macrorhinus leoninus* has double epiphyses in the hand, a discovery which I was myself able to confirm. I found double epiphyses in hand and foot in the following Pinnipedes—*Macrorhinus leoninus*, *Stenorhynchus leptonyx*, *Otaria jubata*, and *Arctocephalus cinereus*; indications in *Trichechus rosmarus*; in the foot only in *Cystophora cristata*.

In the Sirenians, too, I have the same state of things to report. That ossification takes place tardily in these animals also I found from examination of the hand of an embryo 20 centim. in length, in which the terminal phalanges were still cartilaginous, while in the remainder the diaphyses were visible as small round nodules. The consequence of this is that in the adult there is a tendency towards the formation of double epiphyses.

Thus in *Manatus senegalensis* the distal epiphyses of the metacarpals are frequently separate ossifications, while in *Halicore dugong* double epiphyses, which ossify later and are completely separated, are found.

* Allen Thomson, "On the Difference in the Mode of Ossification of the First and other Metacarpal and Metatarsal Bones," Journ. Anat. & Phys. 1869, p. 131.

† Weber, 'Studien an Säugethieren,' p. 170.

‡ Flower, 'Osteology of Mammalia,' 1885, p. 347.

Now it is apparently a deep and impassable gulf which separates the fore limb of all other mammals from that of the whalebone and toothed whales; for while all other mammals have three phalanges on each finger, with the exception of the thumb, which has only two, both kinds of whales have a larger number. This phenomenon is known as hyperphalangy, and no less than three hypotheses have been formulated in recent times in order to explain it. According to the first hypothesis the flippers of whales have no connexion whatever with the fore limbs of land-mammals, but are ancient organs which have been inherited from swamp-inhabiting creatures (*Leboucq*). According to the second theory, the supernumerary phalanges have arisen through the secondary division of a strand of cartilage attached to the last phalanx, such as has been stated to exist in the seals (*Weber*, *Ryder*, *Baur*). The third view is the one recently advanced by Howes *, namely that the supernumerary phalanges arise from intercalary syndesmoses, as in the Amphibia.

It seems to me that none of these three hypotheses are tenable, and in their stead I would suggest a fourth, namely that the hyperphalangy is explicable by the process of double epiphysis formation; owing to the ever-increasing similarity of the various parts and the retardation of ossification, the epiphyses have attained a size equal to that of the diaphyses, and have become equivalent to them. This change took place a long time ago, and no longer admits of direct proof.

I have previously † insisted on the fact that the entire Cetacean finger corresponds to the typical Mammalian finger and that the phalanges only are of different value.

The question will now arise whether we have an instance in nature of the way in which an increase of phalanges takes place. If this process is actually going on anywhere, it must, from what has gone before, be found among the aquatic Mammalia; and it has actually been asserted by Baur ‡ that a fourth phalanx has been found in Sirenia. He writes:—"Flower says, in the last edition of his 'Osteology of the Mammalia,' that the number of phalanges in the Sirenia is never increased beyond the limit usual in the Mammalia—that is, three. But Dr. H. Gadow, in Cambridge, England,

* G. B. Howes, "Observations upon the Morphology and Genesis of Supernumerary Phalanges, with especial reference to those of the Amphibia," Proc. Zool. Soc. London, Dec. 4, 1888, p. 495.

† *Cf.* Anat. Anzeiger, 1888, nos. 22 and 30, and no. 2, 1890; also Denkschriften der medic.-naturwiss. Gesellschaft, Jena, 1889, Bd. iii.

‡ Baur, "On the Morphology and Origin of the Ichthyopterygia," American Naturalist, 1887, p. 840.

showed me a manus of *Manatus americanus* prepared in alcohol, which contained a fourth small ossified phalange in the third digit, and one of *Halicore dugong* which contained an ossified fourth phalange at the fourth and a cartilaginous fourth in the third digit."

Before this Brandt* had described a supernumerary phalanx in *Manatus* and in *Halicore*, and Leboucq † likewise found one on the third finger of the right hand of a sea-cow's skeleton. My own investigations upon this point were not successful: in a manatee-fœtus of 20 centim. I found, as did Leboucq in his fœtal *Halicore*, the third phalanx still completely cartilaginous. Ossification had proceeded very slowly; in the first and second phalanges only small round nodules of bone had formed. Nor did I discover a fourth phalanx in any of the numerous skeletons which I examined; it might, however, have been lost in the process of preparation.

At my request Dr. Gadow forwarded me drawings and detailed descriptions of the above-mentioned fore limbs, from which it appears that in the fourth finger of the *Halicore* there is no joint between the third phalanx and the new nodule of bone, which is therefore to be regarded as a distal bony germ belonging to the terminal phalanx. On the other hand, there is a joint between phalanges iii. and iv. of the third finger. In the same way the third finger of the hand of the manatee shows no joint between phalanx iii. and the new and very small bony nodule.

It follows that we are entitled to speak of a fourth finger-joint in one case only, namely in the third finger of the *Halicore*; in the two other cases a joint between the third phalanx and the new nodule of bone has not yet been found, and the latter is nothing more than the ossification of a distal epiphysis within the cartilage.

There is no question that in the latter case we have the commencement of the formation of a new phalanx.

We have therefore established the fact that a fourth phalanx does occur as a "sport" in the Sirenia. It is very small and not separated from the preceding phalanx, but united with it by cartilage, and can equally well be regarded as an intra-cartilaginous ossified distal epiphysis of the third phalanx. That a true phalanx can arise from it is shown by a case in which a joint is formed between the new nodule of bone and the third phalanx.

* Brandt, "Symbolæ Sirenologicæ," Mémoires Acad. St. Pétersbourg (6e série), Sc. Nat. t. v., 1849.

† Leboucq, "Recherches sur la morphologie de la main chez les Mammifères marins: Pinnipèdes, Siréniens, Cétacés," Arch. Biologie, t. ix., 1889, p. 626.

That which is only commencing to take place in the Sirenia and is found as a rare variation has already been consummated in the whales, and is of quite general occurrence. The original different morphological value of the several secondary phalanges is no longer embryologically visible; but, on the contrary, diaphyses and epiphyses are separated and arise as equivalent pieces of cartilage, while simple symphyses have been formed in place of the joints.

The process of separate epiphysis-formation in the manus of the whale appears to have undergone a further development in a proximal direction. The wrist-bones, which ossify very late, are indeed affected less, or even not at all, though it is stated by Flower * that in the cachalot there exists a species of epiphysis-ossification in the carpus, there being a central nucleus and a peripheral fringe of bone. Much more frequent are the cases in which the radius and ulna form large double epiphyses, the bony centres of which may remain separate. I have already, in the case of an advanced embryo of *Phocœna communis*†, drawn attention to the manner in which it is possible for new skeletal parts to arise owing to this retarded ossification of the epiphyses, and I am now able to allude to the hand of an adult whale ‡, *Hyperoodon rostratus*, in which the double epiphyses of the radius and ulna have developed into independent skeletal elements, with their own bony centres. The tendency towards a formation of epiphyses in the bony parts of the fore arm is already commencing anew, in that a narrow border next to the old epiphysis is incompletely ossified.

We have thus seen how the process of the formation of small skeletal parts, which has long found expression in the case of the fingers, is commencing in the bones of the fore arm also, and that therefore the process is not standing still. We find a further proof of this in the occurrence of double epiphyses on the secondary phalanges. In this case also is retarded ossification the cause of their formation. These secondary double epiphyses, again, may now ossify on their own account, and with this there commences the formation of tertiary phalanges. This process is beginning to take place in certain toothed whales only. Thus I find it in a hand of

* Flower, "On the Osteology of the Sperm Whale," Trans. Zool. Soc. London, vol. vi.

† Kükenthal, "Ueber die Hand der Cetaceen (dritte Mittheilung)," Anat. Anzeiger, 1890, no. 2.

‡ Preserved in the museum of the College of Surgeons, London, the Cetacean material of which institution was most readily placed at my disposition by Prof. Stewart.

Delphinus delphis, where the ossified secondary epiphyses are completely separated from the secondary phalanx; I find the same thing in *Tursiops tursio* and *Lagenorhynchus albirostris*. This process of the formation of tertiary phalanges, which is now progressing, will arrive at completion when the secondary phalanges and the secondary epiphyses shall have attained an equal size; and this will ensue from the progressive retardation of the ossification.

Now, since from the skeletogenous tissue of the fingers in the one case the three phalanges of the typical Mammalian hand are preformed in cartilage, while in the other there results the formation of a number of cartilaginous pieces, the term "phalanx" will gradually lose its meaning for the latter. Functions become simplified more and more, and the finger is built up from a series of small skeletal elements, which are only partially ossified. A distinction of function is perceptible only in so far as the fifth finger of many toothed whales is utilized to an increased extent as a supporting organ. The flipper of the toothed whales is in fact more or less inflected on this side, and the fifth digit has to undertake the task of supporting the expanse of surface which results from the inflexion. We therefore also see how the fifth finger materially exceeds the others in breadth. In consequence of the retarded ossification, which we have established as a process of perfectly general occurrence in the Cetacean flipper, the bony nuclei will no longer suffice for the support of an entire pseudo-phalanx; and we therefore find that they have a lateral origin, and leave a broad cartilaginous mass on the outer side of each phalanx. A further consequence of the great increase in the breadth of the finger is that the separation of the several finger-joints is no longer complete; the dividing groove no longer extends across the entire breadth of the finger, but there ensues a bifurcation on both sides, so that a new cartilaginous piece is detached. With this there commences that splitting-off process, which finally leads to a longitudinal division of the finger. The split-off portions of the newly-formed series now receive bony nuclei on their own account. This splitting-process, authenticated by me in the case of several whales and confirmed by Leboucq, is particularly well seen in certain individuals of the white whale, where I have described it both in the adult and in a small embryo*. Thus the process of the formation of small skeletal parts proceeds, in this case also hand in hand with retarded ossification.

* Kükenthal, "Ueber die Hand der Cetaceen," 1 und 2 Mittheilung, Anat. Anzeiger, 1888, nos. 22 and 30.

With this the climax is reached in the development of the flipper in existing mammals; the modifications of the skeleton become so important that finally the idea of phalanges completely disappears. Not that the transformation-process stops here, however; the changes may proceed yet further, and analogy will show how we have to imagine that this further transformation will take place in the distant future. For we find that in earlier periods of the earth's history there took place the same process of the formation of flippers from the fore limbs of terrestrial animals, namely in the case of the Plesiosauri and Ichthyosauri; while in the latter it reached a much higher degree of development than has yet been attained in existing whales. All that we know about the position of the two groups is that they are not to be regarded as directly connected with one another *, but that both must have sprung from land-reptiles. The latter assertion is opposed to the views of Gegenbaur †, who, on the ground of the resemblance of the extremities, placed them near the fishes; in this he has been recently upheld by D'Arcy W. Thompson ‡. Later discoveries §, however, point with certainty to the conclusion that this resemblance is merely due to convergence and that the ancestors of both groups were land-reptiles. The flipper of the Plesiosauri was the less differentiated of the two; it stood in relation to that of the Ichthyosauri as the flipper of the whalebone whales does to that of the Odontoceti. In the oldest Plesiosaurs the hyperphalangy was still very limited, the separate bones of the hand and the forearm having as yet undergone very little differentiation. I find this in the impression of an as yet undescribed skeleton of a *Mesosaurus* from the Karroo formation ‖ (a *Plesiosaurus* therefore), the hand of which has undergone very little differentiation; its five distal carpals bearing five long metacarpals, to which are affixed two, three, four, five, and four phalanges. The process of retarded ossification makes itself here already perceptible, for *the phalanges carry double epiphyses.* But even the most highly differentiated *Plesiosaurus*-flippers still show a

* Zittel, 'Handbuch der Paläontologie,' p. 478.

† Gegenbaur, "Ueber das Gliedmassenskelet der Enaliosauren," Jenaische Zeitschrift, 1870, pp. 340 *et seq.*

‡ D'Arcy W. Thompson, "On the Hind Limb of *Ichthyosaurus* and on the Morphology of Vertebrate Limbs," Journ. Anat. & Phys. vol. xx., 1886.

§ H. G. Seeley, "On *Neusticosaurus pusillus* (Fraas), an Amphibious Reptile having affinities with the Terrestrial *Nothosauria* and with the Marine *Plesiosauria*," Quart. Journ. Geol. Soc. Lond. vol. xxxviii., 1882. *Cf.* also Fraas, Baur, Zittel, *loc. cit.*

‖ Preserved in the Natural-History Museum, London; Mr. Smith Woodward was kind enough to draw my attention to the specimen.

limited number of phalanges—nine at the most—and distinctly differentiated forearm, carpal, and metacarpal bones. The Ichthyosauri, on the other hand, have a flipper considerably further developed; the process of the division of the finger-rays into a number of small sections has led to a very great hyperphalangy, in addition to which a longitudinal division has set in, such as I have described for the toothed whales, and both processes have undergone further development; the bones of the carpus and forearm too have decreased in size, and in accordance with their simplified function have become mere supporting elements. The most ancient Ichthyosauri, however, show less differentiation in the skeleton of the flipper *; but subsequently we find not only longitudinal division of the fifth digit, but even manifold formation of secondary rays at its side, with dichotomy of other fingers; thus, *Ichthyosaurus longimanus*, for instance, shows four rays one behind the other on the ulnar side, that is nine in all, and in the hand of another *Ichthyosaurus* we find, on tracing the edge of the flipper, as many as fifteen longitudinal rays.

The Ichthyosauri led a life precisely similar to that of the whales. Thus Fraas writes †:—"In the case of *Ichthyosaurus*, where not only the entire carpus, but also the radius and ulna, have been transformed into jointless supporting plates for the flipper, locomotion upon land was absolutely impossible." In consequence of this their limbs were very similar to those of the whales; the flipper of the Ichthyosauri also was ensheathed in a leathery skin; as in the toothed whales the fore flipper was readily bent backwards, and the skeleton followed the curve. Now it seems to me probable, from what has been stated, that the whale's flipper will undergo a further development on the lines followed by that of the Ichthyosaurs, and that the longitudinal fission of the finger of the toothed whales is a process which is as yet in its infancy and which, after further progressing, would finally increase the resemblance to the flipper of the Ichthyosaurs. I therefore regard this longitudinal fission as a new development which is now taking place; and this is a view which I have previously expressed. The explanation of this phenomenon given by Leboucq ‡—" Cette tendence au dédoublement dans le sens longitudinal existant dans certains doigts des cétacés

* *Vide* Baur, "On the Morphology and Origin of the Ichthyopterygia," American Naturalist, 1887, p. 840.

† *Loc. cit.* p. 297.

‡ Leboucq, "Recherches sur la morphologie de la main chez les Mammifères marins," Arch. Biologie, 1889, p. 112.

peut être considérée comme un caractère tout-à-fait primitif" —I can by no means agree to.

To sum up our results. In the aquatic Mammalia there sets in a retardation in the ossification of the skeleton of the hand, a consequence of which is the formation of double epiphyses in each finger-joint. Since each finger-joint thus acquires three divisions, which, owing to reduction, that is the loss of separate functions, become continually more alike, the number of original finger-joints will be doubled. The number of the secondary finger-joints will therefore in the highest case amount to twelve.

The question now suggests itself whether this process can still be followed embryologically. It must be admitted at the outset that this is doubtful, since this transformation took place so long ago, and the principle of making the separate parts resemble one another in form was so speedy in its effect, that it seems practically hopeless to expect that we can still trace the various stages in the development of the embryo. I might express myself in the words of Pfitzner* :—" In osteology in particular is ontogeny an auxiliary as inefficient as it is untrustworthy; we have to rely almost entirely on comparative anatomy and variation." All that we can determine is that from an embryonic tissue there develop pieces of cartilage which are separate from one another and which correspond to the secondary phalanges. There is no question of supplementary division of the cartilaginous tissue; all changes which subsequently took place are traceable to fusion. The whole of the secondary phalanges of the whale's hand are therefore to be found already in their places. Any supplementary division of the cartilage is consequently excluded.

This method of formation renders it impossible to trace the origin of hyperphalangy embryologically; I would only mention that in a very small embryo of *Globiocephalus* there is a considerable difference in size between the secondary metacarpalia and the remaining divisions of the phalanges, in that the former, particularly in the first finger, are very much more minute; in the next stages of development, however, this difference is already obliterated. This difference in size points to the mode of origin of the secondary metacarpal. The fact that it still finds expression here is intelligible when we reflect that the process of hyperphalangy must have commenced at the tip of the finger, and with the division of the original metacarpal has reached its latest stage.

Now if our theory is correct the number of phalanges should

* W. Pfitzner, "Die kleine Zehe," Archiv f. Anat. u. Physiol. 1890, pp. 12 *et seq.*

not exceed twelve in one finger, and this (with a single exception) is in fact the case. No whale exhibits more than twelve phalanges with the exception of *Globiocephalus melas*. In this whale two varieties are distinguishable, in one of which the second finger has twelve phalanges or less, while in the other an increase of phalanges beyond twelve has taken place. We have now to inquire where this augmentation has been effected. According to our theory it must be a third series of phalanges which has been formed by division of the secondary ones, and this moreover at the tip of the finger. This is actually the case; in three embryonic hands I find ten to be the constant number of the phalanges of the third finger; in the second finger, on the contrary, the numbers are eleven, fifteen, and seventeen. In all three the relative position of the first eleven phalanges has not changed in the least; they are to be regarded as homologous with one another. But while the eleventh phalanx is terminal in one case, in another four, and in a third case as many as six, phalanges have been intercalated in front of it, thereby materially altering the arrangement. Where there has been an increase of phalanges the second finger greatly exceeds the third, while it otherwise is of the same length. The increase of segments has therefore affected the tip of the finger in this case.

I must not omit to state that there is nothing to show that the new terminal phalanges have been derived from the proliferation and secondary division of what was previously the terminal phalanx. They are segments which decrease regularly in size, are well separated from one another, and which came into existence as separate rudiments with the earliest development of the cartilage. To my mind we have no alternative but to accept the process of the cleavage of the secondary end-phalanges into tertiary, as resulting from the formation of double epiphyses.

Now it is an apparently inexplicable fact that the whales possess more phalanges in each finger in the immature state than they do in the adult, as has been found to be the case in the whole of the embryos examined by Leboucq and myself with this object; nay, it appears to stand in direct contradiction to my theory of the gradual development of the many-jointed condition. On these grounds it has therefore been also suggested by one investigator of Cetacean anatomy (Leboucq) that the hand of the whale as it is is a very ancient organ.

As a matter of fact, however, the whale's hand is modified by the action of two very different processes, which both exist independently of one another; the one is attributable to the principle of the formation of small skeletal parts, the other comes into action in aquatic mammals, which use their fore limbs no longer for rowing, but merely for steering and balancing purposes. For the latter function a long fore limb is not only unnecessary but even actually in the way; and so a shortening of the limb will take place, which will commence at the distal end. Practical observations are in entire accordance with this; the whole of the Cetacean fingers examined for the purpose show that the diminution in the number of phalanges which takes place in the course of individual development arises from the fusion of the small terminal phalanges.

This fusion of terminal phalanges is also found in other aquatic mammals; thus I was able to determine its presence as a variation in *Manatus senegalensis*, in which it affected the third and fourth fingers.

Now how are we to explain the origin of hyperphalangy phylogenetically?

As the fore limb of the terrestrial ancestors of the toothed as well as the whalebone whales developed more and more into the flipper, the skeleton was also affected thereby, in that a retardation of ossification set in. In consequence of this retardation there arose the formation of double epiphyses, which attained to the size of the diaphysis, while their bony nuclei remained separate. The functions of the finger-joints became more and more alike, in that they had to relinquish all their differences of action and to become modified into mere supporting organs; and this similarity likewise extended to the diaphysis and epiphysis of each finger-joint; they, too, had only to undertake a supporting function. Now the office of the flippers of the whale as rudders entails the avoidance of large bones; and this necessity was met first by retarding the ossification of the diaphyses, and making the two epiphyses equivalent to it, and subsequently by separating the latter from the former; so that in the place of the single skeletal element there develop three similar smaller ones. Where will this process first come into action? Clearly where the retardation in the ossification is most pronounced, and this is the case in the terminal phalanx. The first secondary phalanges will be developed in the terminal phalanx (as, for instance, in the case of *Manatus* and *Halicore*); the further advance of the process affects the other finger-joints also, and finally begins to take place in the bones of the forearm of certain whales. Simultaneously with this process the several division-products grew to resemble one another, owing to their having similar functions to perform; the morphological value of the sections became much less, and we therefore see within the limits of each species a certain amount of variation in their number. The tendency to the formation of small skeletal divisions, to which the retarded ossification and the formation of double epiphyses originally lent an impetus, was at length carried so far that the fingers also began to split in a longitudinal direction, as is seen in the much expanded fifth digit of Odontocetes. In the whales the process of modifying the skeleton of the flipper has not yet said its last word; we see how new double epiphyses are already arising again in the secondary finger-joints and how in the case of a toothed whale, *Globiocephalus*, the same process of increasing the number of segments at the tip of the second finger has already commenced anew, so that therefore it comes in this case to the formation of tertiary phalanges. A portion of the *Globiocephali* do not yet exhibit this process; the majority, on the other hand, have already acquired it.

Precisely the same transformation of the skeleton was experienced in earlier periods of the earth's history by the hands of reptiles now extinct, the Plesiosauri and Ichthyosauri, which likewise became adapted to the aquatic life. In the case of the former the process ceased at a comparatively early stage, much as it is seen in existing whalebone whales; the Ichthyosaurs, on the other hand, carried it much further. While the paddles of some Ichthyosauri (those of the older forms) show the greatest similarity to those of the toothed whales, in the more recent Ichthyosaurs the modification is much greater.

The transformation of the fore limb into the swimming-paddle is therefore regulated by the same laws in widely distant groups. Whalebone whales and toothed whales, Plesiosauri and Ichthyosauri—four groups, not traceable to one another, but originating from different terrestrial ancestors—have acquired precisely similar anterior extremities as a result of the operation of the same laws on the modification of the fore limb. The phenomenon of convergence is here revealed with the utmost distinctness. It appears as if the various flippers were approaching a single type, which has received its fullest expression in the fin of the fish.

Once again we arrive at the conviction, as we have already done in considering the integument of the aquatic mammals, that a large series of resemblances in the structure of the flippers is but the result of convergence, and that it is a mistake to bestow on them phylogenetic value. These must be eliminated if we would compare the extremities of whalebone and toothed whales with one another. After we have recognized the points of resemblance as convergent developments of independent origin the structural differences of the two flippers appear much more clearly defined. The contrast between the much greater advance of hyperphalangy in all the toothed whales and its more limited development in the whalebone whales strikes us at once. But there is also a plastic difference to be noticed, in so far as the whalebone whales possess elongated flippers with a straight radial edge, while in the toothed whales the radial edge of the flipper is more or less curved, so that the flipper has acquired a sickle-like form. This difference is not so trivial as it at first sight appears. It has exerted a powerful influence on the skeleton of the hand. In the whalebone whales the flipper appears to be least modified in the smooth whales (the Balænidæ), where we get a rounder form of flipper whose five fingers are all developed with a very small amount of hyperphalangy; in the fin-whales (the Balænopteridæ), on the other hand, we find an elongated instead of a rounded flipper, with a straight radial edge, and the consequence of this is the degeneration and disappearance of the thumb. Rudiments of it are still seen in the embryo, which afterwards disappear through fusion. Hyperphalangy has already made a certain advance. In the toothed whales, on the contrary, the finger-rays have adapted themselves to the inflexion of the flipper, and the whole of the five digits are always present. Two different types of flippers are therefore observable in the two groups—the whalebone whales with long extended flippers, the toothed whales with incurved ones. In the former the thumb is lost, in the latter it persists. This is already a highly important difference in the structure of the flipper in the two groups. The disposition of the carpal bones constitutes a further fundamental difference. We find that the carpus in the adult in many toothed whales and in the embryonic state in many others exhibits an arrangement which is otherwise not characteristic of the Mammalian class; there are present not only the three proximal but also five distal carpalia, whereas all other mammals only possess four distal carpals; there is a pisiform and a præpollex, while the centrale, which in the rest of the Mammalia is only found occasionally and in embryonic stages, here often persists and is even found double. The number of the carpal elements thus reaches twelve; their arrangement is a perfectly typical one, such as must be imagined for the hypothetical, most complicated, and therefore most ancient Mammalian carpus; and the carpus of the toothed whales displays the greatest agreement with the typical Reptilian carpus, such, for instance, as has been preserved with but little modification in the Chelonia. All this is not found in the whalebone whales, whose carpus consists of remarkably fewer elements. Where changes do show themselves in the carpus they are never cases of fission, but rather of fusion. This observation, which we owe to Gegenbaur, is of universal application; those carpi are therefore to be regarded as the more ancient which exhibit the greater number of component parts. These are the carpi of the toothed whales. We therefore conclude from the comparison of the structure of the carpus in the toothed and whalebone whales that the former animals are the more ancient. If we likewise take into consideration the difference in the manner of the further development of the flippers, we again arrive at the conclusion that the toothed whales were developed from land-mammals at a much earlier epoch than whalebone whales, and that therefore the two groups cannot be directly related to one another.

Our investigations into the structure and development of the flippers have therefore yielded the same result as the investigation of the integument. What were hitherto regarded as resemblances and indications of phylogenetic relationships are merely convergences which have arisen according to the same developmental laws.

With this the series of systems of organs which are modified by adaptation to aquatic life is by no means exhausted, and the studies which I have prosecuted on a tolerably comprehensive material into the dentition, the respiratory organs, &c. contain much that is perhaps of more general interest. Since these investigations, however, have not been entirely concluded, I have confined myself in this paper to a couple of systems of organs. From these the method of investigation may at once be perceived.

The earlier investigations for the purpose of elucidating the phylogeny of the mammals to which I have directed attention have yielded contradictory results, since their proofs were based on a series of common characters. By bringing biology and physiology into the sphere of our observations we have recognized these common characters as resemblances or convergent developments, which have arisen through the adaptation of originally dissimilar organs to new and precisely similar conditions of existence. In the case which we have been considering, the modification of the organs of the various animals is controlled by laws of general application, laws which are even partially attributable to mechanical principles. Now when we thus betook ourselves to the investigation of phylogeny from our altered standpoint, equipped in this instance with a method as yet unused, we were compelled to annul the relations which had hitherto been established, and out of a single Mammalian order even to form two others, genetically very distinct, namely those of the toothed and whalebone whales. And thus we have demolished, instead of reconstructing. Yet we have gained something in return—a firmer basis, on which we may distinguish what is ancestral from that which is newly acquired.

XX.—*Lepidoptera from the Sabaki River, East Africa, with Descriptions of new Species.* By G. F. Hampson, B.A., Coll. Exon., Oxon.

The following is an account of a small collection of Lepidoptera made by Mr. Keith Anstruther, of the British East-Africa Co.'s service, in the Sabaki River district; and as very few species have been recorded from the interior of East Africa, and none from this district, I give a list of them in full. The types of the new species have been presented to the Natural-History Museum.

RHOPALOCERA.

1. *Limnas Klugii*, Bull.

2. *Limnas chrysippus*, Linn.

The small dark African form.

3. *Tirumala petiverana*, Doubl. & Hew.

Mycalesis, subgen. nov. Monotrichtis.

With a glandular pouch and tuft of hairs on both fore and hind wings, thus belonging to Mr. Moore's first group of subgenera of *Mycalesis*.

Allied to the subgenera *Virapa* and *Garesis*. Male with the glandular pouch on the fore wing, a small oval patch below the submedian nervure only, and covered with short scales, and no tuft of long hairs. Fore wing with the apex rounded as in *Garesis*; the inner and outer margins more rounded; costal, subcostal, and median veins swollen at the base; the venation similar. Hind wing with the costa highly arched, as in *Virapa*; the first subcostal much curved up, as in that genus, not swollen at the base as in *Garesis*. Eyes slightly hairy.

Type *M.* (*Monotrichtis*) *safitza*, Hew.